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Social transmission of avoidance among predators facilitates the spread of novel prey

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Warning signals are an effective defence strategy for aposematic prey, but only if they are recognized by potential predators. If predators must eat prey to associate novel warning signals with unpalatability, how can aposematic prey ever evolve? Using experiments with great tits (*Parus major*) as predators, we show that social transmission enhances the acquisition of avoidance by a predator population. Observing another predator's disgust towards tasting one novel conspicuous prey item led to fewer aposematic than cryptic prey being eaten for the predator population to learn. Despite reduced personal encounters with unpalatable prey, avoidance persisted and increased over subsequent trials. Next we use a mathematical model to show that social transmission can shift the evolutionary trajectory of prey populations from fixation of crypsis to fixation of aposematism more easily than was previously thought. Therefore, social information use by predators has the potential to have evolutionary consequences across ecological communities.

Since the first description of aposematism over 150 years ago[1], explaining how these conspicuous warning signals evolve to protect prey in the face of hungry predators remains a challenge[2–4]. Aposematic displays confer little advantage until predator populations associate the prey's display with its unprofitability, and while conspicuous signals are easy to detect and facilitate rapid learning[5], this feature also means they are often taken much more readily than cryptic prey during predator education[5,6]. If all predators must consume novel conspicuous prey to learn, then aposematism is unlikely to evolve[2], and it cannot be maintained easily if immigrants or juvenile predators are naïve[7,8]. This becomes particularly problematic when prey are lethal, as predators have no opportunity to learn from their foraging mistakes[9]. Nevertheless, aposematism is a widespread defence with multiple evolutionary origins, showing that it can establish across diverse predator–prey systems[10,11].

Many factors might assist aposematic phenotypes in overcoming this cost of conspicuousness to reach fixation in prey populations[11], although experiments in the laboratory and field suggest the puzzle is yet to be fully resolved[4]. For example, aggregating reduces attack rates endured by unpalatable prey[12], but predators still require repeated encounters with prey aggregations to learn avoidance[12], and aposematic displays are more common among non-aggregating prey[3]. Wariness of novel food items may confer an initial advantage for aposematic prey[11]. However, experiments demonstrate that dietary conservatism is rarely sufficient to reduce the initial predation risk below that of cryptic phenotypes[13], and social effects during foraging encourage predators to become less conservative about incorporating novel foods into their diet[14]. Even innate biases against common warning signals (for example, black and yellow stripes) are insufficient to protect novel prey completely: novel aposemes suffer higher mortality overall than cryptic phenotypes[13], perhaps because reinforcement is required for predators' initial biases to become avoidance[15], and juvenile predators can show less aversion to novel prey than adults[7,15]. Furthermore, when a predator's nutritional state declines, it increases its consumption of unpalatable prey[4], meaning that aposematic prey in the wild continue to face predation[8], even when some of the population is educated[16].

Considering the information ecology of aposematism[17] may help reconcile how it evolves and persists. When encountering novel prey, predators face uncertainty about its palatability and nutritional benefit[4] so, in theory, they should acquire as much information as possible before risking consumption[17,18]. Previous work has focused on predators becoming educated about warning signals through interacting with and consuming prey themselves[4] (that is, personal information), perhaps influenced by innate preferences and biases against colours or patterns[15], or wariness of unusual foods in general[11]. However, paying attention to the foraging behaviour of others (that is, social information[17]) could provide an additional potent source of information[19]. Social transmission of food aversions has been demonstrated in a range of taxa: for example, vervet monkeys learn to prefer palatable rather than unpalatable foods by observing educated troop members[20], juvenile great tits increase their avoidance of aposematic prey if they observe an adult eat an alternative[21], and tamarin monkeys[22], red-winged blackbirds[23], house sparrows[24] and domestic chicks[25] avoid foods after observing a conspecific show distress. Observing another's characteristic response to distasteful food can also increase chickens' wariness of two typical colours used by aposematic prey[26]. However, whether social transmission facilitates the evolution and spread of novel conspicuous prey compared with an alternative phenotype[27] remains untested.

Here we combine experiments with a mathematical model to test whether social transmission of avoidance among predators enables novel aposematic prey phenotypes to reach fixation more readily than was previously assumed. We used the novel-world method[5,28] where naïve predators search in an artificial landscape for artificial prey (paper packets containing food) marked with novel signals that are either cryptic (they share the signal printed on the landscape) or conspicuous[5,28]. The palatability of prey is manipulated by soaking small pieces of almond in chloroquine phosphate—a mild toxin that facilitates associative learning[29]. This method avoids using signals that are found in a predator's current environment or

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Box 1 | Modelling the evolutionary consequences of social transmission for prey phenotypes

We consider a population of predators and prey that inhabit either a single habitat patch (site) or several. In the case of several patches, they are linked by migration of both predators and prey (see 4 below). The focal prey species has two possible morphs—palatable cryptic (C) and unpalatable aposematic (A)—which are inherited from parent to offspring. We denote the population density of cryptic prey at site i at time t as $C_i(t)$ and aposematic prey as $A_i(t)$ (i and t are dropped from notation where it improves clarity). Being aposematic increases the attack rate, denoted a, by a factor α, which means that in a starting population of N predators, C cryptic prey and A aposematic prey, attacks occur at a rate $aNC+\alpha aNA$. The population dynamics are governed by interactions between each of the following processes:

Naïve predators can become educated via personal experience with distasteful prey (1)

Predators are born naïve ($N_i(t)$) before becoming educated ($E_i(t)$); a single encounter with an aposematic prey item makes the predator educated with a probability p, and an educated predator will not touch aposematic prey again (thus it takes on average $1/p$ encounters for the transition to happen). When a proportion p of encounters with aposematic prey leads to predators leaving the state 'naïve' and arriving at the state 'educated', the total rate of individuals experiencing this transition, measured at time t, equals $p\alpha aN(t)A(t)$. If there are no naïve predators left, or if there are no aposematic prey to be encountered, no predator can become educated.

Naïve predators can become educated predators via social transmission (2)

Focal predators can observe the foraging of b—other individuals who reside in the same habitat patch (cases with $b>0$ are called social transmission scenarios). The parameter q ($0\leq q\leq 1$) specifies the efficiency of social transmission, relative to personal experience (i.e. p). If, for example, $p=0.5$ and $q=0.1$, personal experience with a distasteful item leads to future avoidance with a probability of 50%, but watching another individual react the same way only leads to $qp=0.05$ probability (that is, 5%) that this transition happens for the observer. If $q=1$, watching is equally efficient as personal experiences: $qp=p$ in this case.

We make the conservative assumption that social transmission occurs only after observing others transition from naïve to educated, and observation effort is not specifically directed towards naïve individuals. The computations necessary are thus that each of these other individuals (b) is currently naïve with a probability of $N/(N+E)$; therefore, each focal predator is offered 'social transmission opportunities' at a rate of $q\alpha apbN/(N+E)$, and the total number of transitions happening through social transmission is obtained by multiplying by N, the density of naïve observers capable of following this route.

Prey die because of predation, and predators may also die. Both experience logistic population growth towards their carrying capacity (K_{prey} or K_{pred}) (3)

All attacks are assumed fatal for the prey, whether or not a predator becomes educated. Because only naïve predators attack aposematic prey, the per capita deaths of aposematic prey equal α aN, leading to density changes $(-\alpha aN+r_{\text{prey}}(1-(A+C)/K_{\text{prey}}))A$ for aposematic prey. The corresponding change for cryptic prey is $(-a(N+E)+r_{\text{prey}}(1-(A+C)/K_{\text{prey}}))C$. Here, r_{prey} denotes the intrinsic growth rate of the prey population and the term $(1-(A+C)/K_{\text{prey}})$ describes density dependence leading to logistic growth where aposematic and cryptic prey are assumed to contribute identically to density dependence.

The mortality rate of predators, μ_{pred} for all predators, is assumed to be independent of whether predators are educated or not. Predator mortality may occur due to causes other than encounters with the focal prey species and we allow for the density of naïve individuals to increase when there is turnover in the predator population (all individuals being naïve at birth). Population growth towards carrying capacity is therefore added to naïve predator density, leading to a population growth term $-\mu_{\text{pred}}N+r_{\text{pred}}(1-(N+E)/K_{\text{pred}}))(N+E)$ for naïve predators and $-\mu_{\text{pred}}E$ for educated predators.

Migration (4)

Per capita migration rates equal m_{pred} and m_{prey} for predators and prey, respectively. Migration is assumed to lead to individuals emigrating from their natal patch and landing in any other patch, which means that the net immigration for patch i, exemplified for naïve predators, is

$$-m_{\text{pred}}N_i+\frac{m_{\text{pred}}\sum_{i=1}^{k}N_i}{k}$$

if there are k patches in total.

When processes 1–4 occur simultaneously, the system as a whole obeys the following equations:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t}=-p\alpha aN_i(t)A_i(t)-\frac{q\alpha apbN_i(t)^2}{N_i(t)+E_i(t)}-\mu_{\text{pred}}N_i(t)+r_{\text{pred}}\left(1-\frac{N_i(t)+E_i(t)}{K_{\text{pred}}}\right)(N_i(t)+E_i(t))-m_{\text{pred}}N_i(t)+\frac{m_{\text{pred}}\sum_{i=1}^{k}N_i(t)}{k}$$

$$\frac{\mathrm{d}E_i}{\mathrm{d}t}=p\alpha aN_i(t)A_i(t)+\frac{q\alpha apbN_i(t)^2}{N_i(t)+E_i(t)}-\mu_{\text{pred}}E_i(t)-m_{\text{pred}}E_i(t)+\frac{m_{\text{pred}}\sum_{i=1}^{k}E_i(t)}{k}$$

$$\frac{\mathrm{d}C_i}{\mathrm{d}t}=-a(N_i(t)+E_i(t))C_i(t)+r_{\text{prey}}\left(1-\frac{A_i(t)+C_i(t)}{K_{\text{prey}}}\right)C_i(t)-m_{\text{prey}}C_i(t)+\frac{m_{\text{prey}}\sum_{i=1}^{k}C_i(t)}{k}$$

$$\frac{\mathrm{d}A}{\mathrm{d}t}=-\alpha aN_i(t)A_i(t)+r_{\text{prey}}\left(1-\frac{A_i(t)+C_i(t)}{K_{\text{prey}}}\right)A_i(t)+r_{\text{prey}}\left(1-\frac{A_i(t)+C_i(t)}{K_{\text{prey}}}\right)C_i(t)-m_{\text{prey}}C_i(t)+\frac{m_{\text{prey}}\sum_{i=1}^{k}C_i(t)}{k}$$

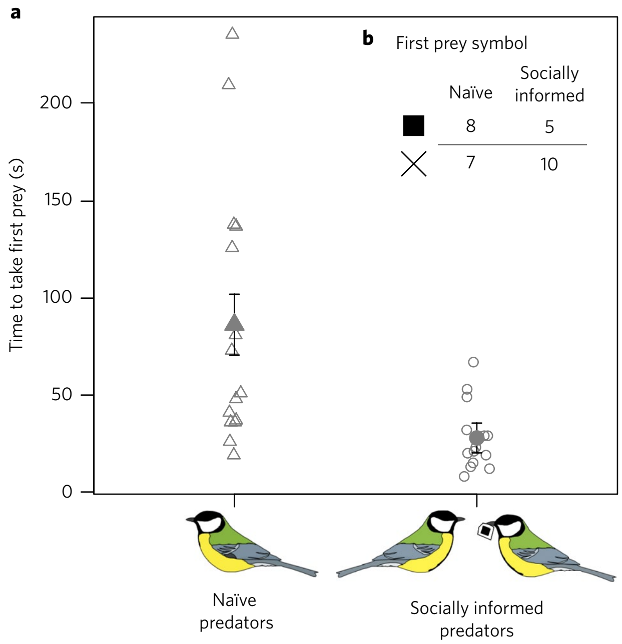

Fig. 1 | Latency to forage and initial prey choices. a,**b**, Socially informed predators foraged more quickly for their first prey item (**b**; unpalatable conspicuous square signal versus palatable cryptic cross signal) than naïve control predators. Filled symbols in a show means (±s.e.) from a negative-binomial mixed-effects generalized linear model including a random intercept for cohort. One socially informed predator was excluded (latency = 644 s, effect of social information with outlier included = –0.71 ± 0.36, χ^2 = 3.81, d.f. = 1, P = 0.05; Supplementary Table 1). In **b**, the difference in the initial prey symbol taken was not significant (effect of social information on the odds of the predator taking cryptic prey first = 0.91 ± 0.82, χ^2 = 1.34, d.f. = 1, P = 0.25; Supplementary Table 1).

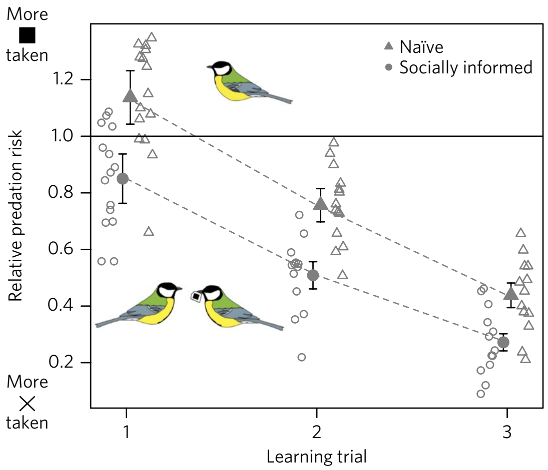

Fig. 2 | Relative predation risk for novel conspicuous prey versus the cryptic phenotype. The mean (±s.e.) number of aposematic prey consumed divided by the number expected by chance during three learning trials over consecutive days (one trial per day). Great tits with social information about prey signals (circles, n = 15) consumed relatively fewer aposematic (conspicuous unpalatable square signal) than cryptic (palatable cross signal) prey compared with birds with no social information (triangles, n = 15). The open symbols show individual variation in foraging choices and the solid reference line indicates equal predation of the cryptic and aposematic prey types. The plotted data were derived from a mixed-effects binomial generalized linear model including a random intercept for cohort and slopes for each individual.

in its evolutionary past. We used great tits *Parus major* as our model predator because they learn from personal encounters to avoid novel artificial[5,28] and real aposematic prey[7,30], and also use social information for foraging: they copy foraging locations[31] and acquire new foraging skills by observing others in the wild[32]. Like many bird species[33], great tits respond to distasteful prey items by shaking their head and wiping their beak vigorously on a nearby perch (Supplementary Videos 1 and 3); using video playback, we provided half of the predators with this potential source of social information about signals and unpalatability before they encountered the prey population. We predicted that socially informed predators would (1) forage for novel prey more quickly than naïve predators without social information[33] and (2) consume fewer conspicuous than cryptic prey despite them being almost three times more visible to predators[5]. If social information is to facilitate the evolution of novel aposematic prey, avoidance must persist during multiple encounters with prey populations. Therefore, we repeated our experiment on two subsequent days (but without further video playback) and predicted that socially informed predators would (3) continue to avoid unpalatable prey, despite fewer opportunities for personal learning and feedback from toxin ingestion[4]. We then used a mathematical model (Box 1) to investigate the evolutionary consequences of social transmission for a spatial mosaic of prey populations.

Results

Socially informed predators were quicker than naïve control birds to select their first item from the prey population (effect of social information = –1.13 ± 0.24, statistical datum derived from a likelihood ratio test (χ^2) = 20.06, d.f. = 1, P < 0.001; Fig. 1a and Supplementary Table 1) and 67% ate a cryptic prey item first compared with 53% of predators naïve to the unpalatability of the conspicuous symbol (Fig. 1b and Supplementary Table 1). This suggests that socially informed predators were not foraging more quickly simply because they had observed a conspecific, but that social information encouraged quicker decision-making. Observing another predator consume just one unpalatable prey item subsequently resulted in a 32.1% reduction in predation risk for the novel aposematic phenotype (Fig. 2): focal birds presented with social information consumed fewer aposematic prey items than the alternative cryptic form during the first trial compared with birds that needed to learn through trial and error only (Fig. 2; effect of social information = –0.65 ± 0.23, χ^2 = 7.98, d.f. = 1, P = 0.005; Supplementary Table 2). Adult male great tits (our demonstrators) are dominant over juveniles and females[34], yet conspicuous prey enjoyed similar protection from socially informed predators regardless of the age of the observer (adult versus juvenile observers = 0.22 ± 0.47, χ^2 = 2.38, d.f. = 1, P = 0.63) or whether they were subordinate to the demonstrator (adult male versus subordinate observers = 0.60 ± 0.45, χ^2 = 2.03, d.f. = 1, P = 0.15).

During subsequent encounters with prey populations, we found that all birds continued to learn to avoid aposematic prey (effect of trial number = –0.77 ± 0.12, χ^2 = 24.00, d.f. = 1, P < 0.001; Supplementary Table 2). Regardless of the information available, birds improved across trials at a similar rate (information × trial number: χ^2 = 0.14, d.f. = 1, P = 0.71) despite differences in the amounts of unpalatable prey ingested (effect of social information = –0.58 ± 0.18, χ^2 = 12.13, d.f. = 1, P < 0.001; Supplementary Table 2). Therefore, when experimental prey populations were under selection from socially educated predators, the aposematic phenotype was more likely to persist than the cryptic form, even across subsequent days (Fig. 2).

Our experiments provided ample opportunity for socially informed birds to also learn through personal experiences: the artificial prey population was already 50% aposematic[5]. In nature, however, the proportion of aposematic prey present varies, which affects the chances for observers to witness and learn from predation events. Therefore, next, we investigated the expected evolutionary consequences of social transmission using a modelling approach (Box 1) through which we varied (1) the initial proportion of the population that was aposematic, (2) the cost of conspicuousness and (3) the number of predators learning by observing a predation event, relative to the probability of learning from a single personal encounter with distasteful prey. We assumed that the predator was not a specialist on the focal prey species, and our model implicitly assumed the availability of alternative palatable prey.

The positive effect of social transmission on prey survival detected in our experiments also affected, at suitable parameter settings, whether crypsis or aposematism was selected to fixation (Fig. 3; the depicted 20% initial aposematism is above the threshold if individuals learn from others, but below it if they do not). Fixation of the aposematic phenotype required crossing a wider invasion barrier: if abandoning crypsis means prey are much more visible (high α; Fig. 4), warning colours should be common to begin with. However, when conspicuousness (α) was higher, the benefit conferred by social transmission was also larger (it was able to reduce the width of invasion barriers the most where these were widest; Fig. 4). As a net effect, however, the smaller reduction apparent at low α might matter more for fixation because narrower invasion barriers are, as a whole, more likely to be crossed.

Prey and predators occur across a spatial mosaic of meta-populations, which could influence the dynamics and effects of social transmission; avoidance learning may not necessarily occur at the same rate at every site[35] and educated predators may also migrate among prey populations, reducing predation pressure on local prey populations[35]. Therefore, we next added migration and stochasticity to the model to investigate how social transmission influenced the chance that aposematic phenotypes would reach fixation. We found that immigration from neighbouring sites that have already crossed an invasion barrier can potentially aid a local population to cross it too (red area in Fig. 5). Spread is facilitated because prey subpopulations can now cross the invasion barrier sequentially: the first subpopulation to do so makes aposematism locally fixed, and aposematic individuals thereafter constantly spread to nearby habitats. Social transmission helps the first subpopulation to reach fixation, which then facilitates other subpopulations to also cross the barrier. Conversely, prey populations that do not enjoy social transmission of avoidance among predators have to rely on other

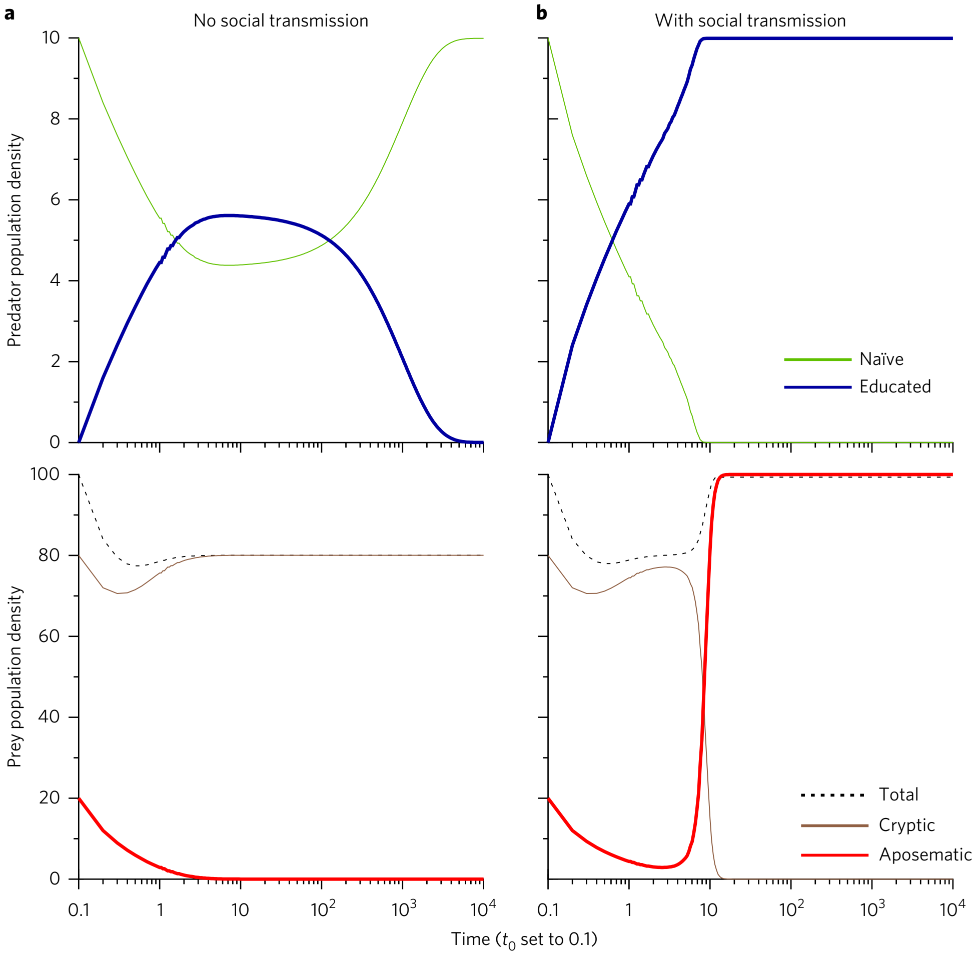

Fig. 3 | An example of the temporal dynamics predicted if social information is available. We assume all predators are naïve at $t=0$ and that aposematic prey are four times ($\alpha=4$) easier to detect than cryptic prey and comprise 20% of the initial prey population. **a**, When social information is not used ($b=0$), the proportion of naïve predators (green line) becomes less than that of educated predators (blue line); however, aposematism vanishes because naïve predators are still present and detect aposematic prey (red line) more easily than cryptic prey (solid grey line). **b**, Conversely, social transmission ($b>0$) leads to a faster decline in naïve predators. Once a sufficient proportion of predators are educated, the net growth rate of the aposematic population is faster than that of their cryptic competitors and aposematism fixes (dashed grey line). Any new naïve predators become educated almost instantly (by personal learning) because aposematic prey are now very common. Here, we use $b=5$ to demonstrate the effect (only threshold frequency varies with this value). Other parameter values: $a=0.1$, $p=0.2$, $q=0.1$, $\mu_{\text{pred}}=0.001$, $r_{\text{prey}}=5$, $r_{\text{pred}}=1$, $K_{\text{prey}}=100$ and $K_{\text{pred}}=10$.

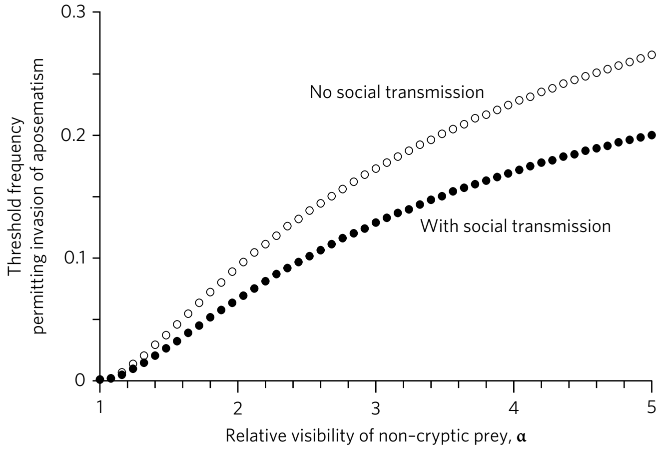

Fig. 4 | Threshold frequency of aposematic prey necessary for the phenotype to reach fixation. Social transmission (filled circles) reduces the threshold frequency of occurrence that aposematic prey must be present at for the phenotype to invade the prey population (compared with personal information only (open circles)). Starting populations are created from different initial frequencies for the aposematic type (between 0 and 30%) to seek the threshold frequency that is necessary for subsequent fixation. From Fig. 3, we know that the threshold for $\alpha = 4$ must be located higher than 0.2 if there is no social transmission and lower than 0.2 if there is social transmission. Here, we seek the exact threshold. Parameter values, except for α (which is now varied), are the same as those in Fig. 3.

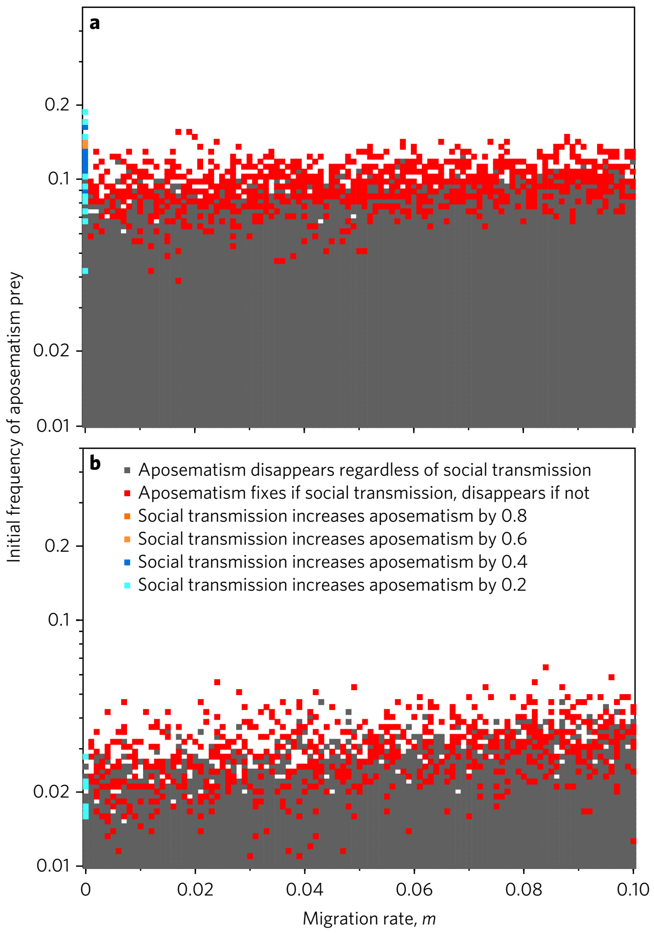

Fig. 5 | Effect of social transmission on the initial population size required for aposematic prey to reach fixation. Whenever there is migration (all cases with $m > 0$), there is a range of initial population sizes (marked red) at which aposematism only fixes if social transmission is possible ($b > 0$). **a**, This range of initial frequencies is higher where we 'seeded' five subpopulations with 100 individuals binomially chosen to be aposematic or not. **b**, This range of initial frequencies is lower where the 500 individuals ($K_{\text{prey}} = 100$ at 5 sites) were additionally grouped to form subpopulations with maximum local association of aposematic prey. Thus, if, for example, an initial frequency of 0.2 led to 104 aposematic individuals, subpopulation 1 was assumed to be 100% aposematic, subpopulation 2 had 4 aposematic individuals (4%) and the remaining subpopulations had none. Initial frequencies of aposematism ranged from 0.01 to 1, but we do not show values above 0.5 as they always led to fixation, regardless of the scenario. Parameter values: $\alpha = 2.5$. The other parameters are the same as those in Fig. 4.

processes[35] to help aposematism cross the (now higher) threshold and spread towards fixation.

Discussion

If predators have access to social information about prey palatability and signals, our empirical and theoretical results suggest that aposematism can arise more easily: (1) social information reduces the initial frequency of aposematic prey required for predator populations to become educated, (2) it can also have an effect even when signals are moderately conspicuous and (3) migration of predators and spatial assortment of prey types increases the strength of these effects. Using social information during foraging is a widespread phenomenon, from insects[36] to fish[37], reptiles[38] and mammals[39]. While demonstrating avoidance is influenced by observing the interactions of others with unpalatable foods is limited thus far to a few species of mammals[20,22] and birds[21,23,26], the cognitive processes involved in acquiring avoidance asocially are unlikely to be different from learning socially[40]. This means that social information has the potential to influence how many species acquire avoidance. While our experiments used great tits as a model predator, the positive effects we detected of social transmission for novel prey phenotypes could occur across a wide range of predators and prey.

Our experiments and model were conservative: we gave observers in our experiment only one opportunity to gather social information, and naïve predators could only observe others showing a disgust response once they took an aposematic prey item. Social transmission may also occur, however, if animals observe the foraging decisions of already-educated group members[20,21] and there is growing evidence that individuals adopt the majority foraging choices of a group[20,32]. Furthermore, aposematic prey may sometimes survive predator attacks[41]; although we did not consider 'taste-rejection' in our experiments or model, this might also provide social information and enhance the personal learning of predators. Rejected prey would also re-join the prey population and therefore have the potential to educate again. Field experiments recording social transmission and prey survival are required to assess whether these processes occur among predator populations. If present, social information could have even stronger effects for aposematic prey in nature than what we detected here.

Is social learning necessary for social transmission of avoidance? Our experiments did not allow us to assess the exact cues used by observers to adjust their foraging decisions, so observers might have been reluctant to eat the demonstrated signal only to avoid perceived competition (all of the demonstrators used were adult males), for example. However, subordinate great tits will readily move towards a food source once a more dominant bird has moved[34] and during the testing phase birds foraged alone. Alternatively, observing another individual encounter something unpalatable might have encouraged predators to avoid the more conspicuous option by simply increasing neophobia[26] or fear[42]. However, our data suggest that predators associated social information with the conspicuous prey signal. 'Socially informed' predators consumed fewer aposematic prey than naïve control birds during the first day, meaning they had fewer opportunities to associate prey signals with palatability directly[4]. If social effects were the cause of the initial reduction, predation risk should have increased during the second day of the experiment to be the same (or higher) than in the control group. We detected the opposite: socially informed predators continued to avoid the aposematic prey more than the control group across all three days of the experiment. In addition, both cryptic and conspicuous prey signal types were novel to the birds and, during the video validation experiment, focal birds chose to eat from a less preferred cup after observing a disgust response (Supplementary Fig. 1). Together, this suggests that social learning is the more likely explanation, but further work is needed to pinpoint the units of information.

Social transmission of knowledge about warning signals is likely to interact with other mechanisms and conditions suggested necessary for the evolution of aposematism. Wariness of novel foods by predators, for example, could help rare aposematic phenotypes to evolve if it reduces initial attacks[11,15], but dietary wariness varies within predator populations[13] and initial wariness requires negative feedback to persist[2]. Social transmission, however, could resolve this if warier individuals learn avoidance by observing the foraging of less wary predators, rather than eventually consuming prey themselves[2]. Social information may also be more readily available if prey are aggregated, enhancing the proposed positive effects of aggregations for the evolution of aposematism[3] (Fig. 5a). Predators also aggregate, and flocking among birds facilitates transmission of information about food[43]. In addition, flocks commonly include heterospecifics[44] who may have different propensities to try novel prey items[7]. This means there could be local variation in the social information available to naïve predators, perhaps explaining why aposematic signals vary among predator communities[45]. Furthermore, even educated predators sometimes taste aposematic prey[4] (Fig. 2); this too could provide local knowledge about prey signals for any naïve immigrants[8,16].

Our findings indicate that social interactions within species may have broad implications for understanding interactions among species[46]. For example, range expansion of predators or their prey can lead to populations that are naïve to prey defences. This often has disastrous consequences, but sometimes avoidance occurs much more rapidly than expected[47]. Variation in social behaviour and predators' propensity to learn by observing others could help explain why some species have been able to associate toxicity with novel prey rapidly and consequently avoid consuming them[48]. Despite growing awareness that social networks influence how species learn about their environment, the emergent properties of social transmission for interacting species are only beginning to be realized[46,49,50]. Our study demonstrates that social transmission among predators has the potential to influence the evolutionary trajectories of prey. Understanding the complexity of coevolution therefore requires an appreciation of the social dynamics taking place within, as well as between, interacting parties.

Methods

Predators and housing. Wild great tits (*P. major*) were caught from October 2013 until January 2014 using traps at feeding stations (containing peanuts) in forest at the University of Jyväskylä Research Station, Konnevesi, Finland (62.6° N, 26.3° E). We controlled for variation in observer–demonstrator familiarity by catching birds in groups of five and always within two hours (immigration and emigration rates are high during Finnish winters[51]). Groups always included at least one adult male (who was used as the group's demonstrator during our experiments), but used juveniles (first year) and adults (older than the first year) and both sexes in foraging tests. Adult males are more common in this population so we used them as demonstrators to reduce heterogeneity and because subordinate great tits are known to pay attention to the foraging behaviour of more dominant birds (adult male great tits are dominant over juveniles and females)[34]. All birds were naïve to our experimental treatments (every great tit caught and released at the research station is ringed) and assigned alternately, but not by catching order (experimental data collected by R.T.).

Great tits were housed indoors in individual plywood cages (65 cm × 50 cm × 80 cm) with a daily light period of 11.5 h (lights on automatically between 08:30 and 20:00 Eastern European time). Birds had acoustic contact only. They were provided an ad libitum supply of fresh water, sunflower seeds and tallow, but were food deprived before the experiments for 2 h to ensure motivation to search for prey. Water was always available. Our experiments were conducted with permission from the Central Finland Centre for Economic Development, Transport and the Environment (KESELY/1017/07.01/2010) and license from the National Animal Experiment Board (ESAVI-2010-087517Ym-23). No birds died in captivity and all were released at their site of capture following the experiments.

The 'novel-world' experimental arena. We used an established protocol[5,28] to test for differences in relative predation risk between cryptic and conspicuous prey signals. The floor of the aviary (3.0 m × 3.5 m) was covered in white paper sheets printed with 71 × 80 small black crosses and laminated to protect the surface. An additional 100 three-dimensional 'fake prey' (white paper squares with a cross symbol, 8 mm × 8 mm) were stuck randomly across the surface (using white double-sided adhesive foam tape). This enhanced crypsis of the prey that shared the cross symbol (see below). The floor was divided into eight rows using wooden planks; this allowed us to assign a grid reference to the floor so we could note where birds selected prey, and provided great tits with positions to inspect prey. Two perches were also provided on the walls of the aviary on which the birds consumed their chosen prey. The foraging choices of the birds were observed via a one-way glass window in the door to the aviary.

Artificial prey. Prey were small pieces of almond (approximately 0.1 g) glued (using a non-toxic UHU glue stick) inside a white paper packet (8 mm × 8 mm). Packets were printed on both sides with a black symbol to act as a signal of the contents. Cryptic prey were printed with a cross, whereas conspicuous prey were printed with a square that made them three times more visible to the birds[5]. Conspicuous prey were made highly unpalatable by soaking the almond slices for 1 h in a solution of 30 ml water and 2 g chloroquine phosphate before air drying; great tits learn to associate signal type with prey distastefulness at this concentration[29].

Training procedure. Following a four-step procedure that has been described elsewhere[13], we trained demonstrators and observers to handle our artificial prey. We used plain white packets during training and birds could not progress to the next stage until they had opened and consumed five prey. All birds learned to open prey within one day. Next, we trained the birds to forage in the novel world. First, each catch-group was housed together overnight in the aviary to accustom them to the room and encourage them to forage from the floor. Sunflower seeds and peanuts were available on the floor to encourage them to forage (fresh water was always available), but plastic sheeting obscured the floor. This also ensured that observers were familiar with the demonstrator of their catch-group. The second stage of training introduced birds to the novel landscape and the presence of cryptic prey. We placed nine plain white prey in three groups, along with one group of three cross-symbol prey, in random locations. For each group, one prey item was on the wooden plank and was therefore highly visible, while the others were on the paper background and consequently harder to find. Using three cross-type prey ensured that all birds knew how to forage in the novel world, but minimized experience with the signal. All birds were trained individually and in an identical fashion, so there were no differences among experimental treatments in their experience with artificial prey before video playback. Training was complete once birds had found and consumed all 12 prey.

Using video playback to provide social information. Video playback minimizes variation in demonstrator behaviour across replicates[33], alters the foraging behaviour of blue tits[33] and has been used successfully to manipulate social conditions in great tits[52]. Nevertheless, before our main experiment, we validated that video playbacks led to changes in great tits' foraging behaviour (Supplementary Methods and Supplementary Fig. 1).

Before filming, demonstrators were habituated to the test chamber: a wooden box (50 cm wide × 50 cm deep × 67 cm high) with a tinted plexiglass front containing one horizontal perch and fresh water at all times. The box was illuminated by a single energy-saving fluorescent light and was placed in a dark room with no other lighting. This ensured that the demonstrator was easily observable, and could be filmed, but that the birds could not see us. Videos were recorded using a high-definition camcorder (Canon Legria HF R37) positioned 1 m away and centred in front of the box. After filming, demonstrators were returned to their home cages (with ad libitum food and water), monitored overnight and then released back into the wild.

Demonstrators were provided with a square-symbol prey item for filming. This was placed at an angle of around 45° on the floor of the test box (by leaning it against a small piece of adhesive putty (Blu-tack) and was 15 mm × 15 mm (to enhance visibility in the video). To ensure a highly visible disgust response and to minimize heterogeneity among demonstrators[53], we made the prey item as distasteful as possible by soaking the almond piece in a saturated solution of 4 g chloroquine phosphate and 30 ml of water for 1 h before being left to dry. Videos consisted of the demonstrator perching next to the prey item, before taking it in its beak to the box's perch. There, the prey was held between the perch and the bird's foot while the packet was opened, allowing a good view of the prey and its symbol. Upon tasting the almond piece, most birds dropped it before wiping their beaks vigorously (Supplementary Video 3). We then edited the videos (using iMovie version 10.0) to include 1 min 30 s of the demonstrator investigating the prey, attempting to consume it and beak wiping (median beak wipes = 39.5, range = 17–59); the beginning and end of the video was spliced with a 30 s clip of the cross-symbol prey (but with no demonstrator present). This ensured that any avoidance or attraction to the cryptic prey was not because of either neophobia or neophilia. See Supplementary Videos 3 and 4 for examples.

Predation experiment protocol. Each bird was tested once per day, over three consecutive days (see Supplementary Fig. 2 for set up). Before our experiment, individual birds were housed for 2 h in a test box in the corner of the room, identical to that used during filming of the demonstrator, and provided with water only. The liquid-crystal display monitor was positioned in front of the Perspex screen, so birds were habituated. Immediately before the first test, observers were shown a video; 15 birds in the 'socially informed' group (4 females, 11 males; 8 adults, 7 juveniles) observed the demonstrator responding to the square prey, while 15 birds in the 'naïve' control group (6 females, 9 males; 6 adults, 9 juveniles) observed a video of identical length, but with 1.5 min of each prey type without a demonstrator present (Supplementary Video 4). Our control videos included the prey to ensure that naïve and socially informed birds were similarly experienced with the prey symbols, but did not include a demonstrator because a bird ignoring prey may also have provided social information about unpalatability[21].

Birds were then allowed to move into the aviary by removing the Perspex screen and controlling the lighting in the test box and in the aviary room (like most birds, great tits are immobile in the dark but move quickly towards light). We recorded when each bird left its box to explore the aviary as the start time for the experiment (there was no difference between experimental groups in their motivation to begin the experiment; $\chi^2 = 0.13$, d.f. = 1, $P = 0.72$). The novel landscape was divided into four quadrants, and six of each prey type were scattered randomly across each (24 cryptic prey and 24 conspicuous prey in total for each trial). The type of prey and its location were noted so we could ensure that we recorded the foraging choices accurately. Birds were allowed to eat 25% of prey in each trial (12 of 48 prey) and we noted the time (s) and identity of each prey item taken. A predation event was recorded if a package was opened.

Statistical analyses. We used generalized linear models with error distributions appropriate to the data structure and included a random intercept term to account for potential variation among catch groups. There were twice as many males as females in our experiment, which precluded analysing sex differences in response to treatment. Analysis of the predation experiment used a binomial error distribution to model a response term where the number of aposematic prey and cryptic prey consumed were bound, and also included a random intercept and slope for each individual over the three trials. Differences in motivation and latency to take the first prey item used a negative-binomial error distribution to account for skew. We ran each analysis by using Akaike's information criterion corrected for small sample sizes to rank a model containing the experimental treatment (in interaction with the trial number where appropriate) against candidate models that each included an additional variable of interest (date during experiment, adult versus juvenile, latency to enter aviary and whether the individual had been used in a validation experiment; Supplementary Tables 1 and 2) and a null model. The model with the lowest ranked Akaike's information criterion corrected for small sample sizes was retained and the significance of its terms assessed using likelihood ratio tests compared with a χ^2 distribution (model outputs in Supplementary Tables 1 and 2). All analyses were conducted in R version 3.4.0 (ref. [54]) using the lme4 package (ref. [55]) and we plotted predicted values to account for the effects of random terms. Supplementary Fig. 3 presents the raw data from our experiment.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. The datasets generated during the study are available from the Natural Environment Research Council's Environmental Data Centre (https://doi.org/10.5285/db55406b-c9a1-4a9e-88c2-2abbcb4bcad3).

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References

1. Poulton, E. B. *The Colours of Animals: Their Meaning and Use Especially Considered in the Case of Insects* (Kegan Paul, Trench, Trübner & Co., London, 1890).
2. Puurtinen, M. & Kaitala, V. Conditions for the spread of conspicuous warning signals: a numerical model with novel insights. *Evolution* **60**, 2246–2256 (2006).
3. Ruxton, G. D. & Sherratt, T. N. Aggregation, defence and warning signals: the evolutionary relationship. *Proc. R. Soc. B Biol. Sci.* **273**, 2417–2424 (2006).
4. Skelhorn, J., Halpin, C. G. & Rowe, C. Learning about aposematic prey. *Behav. Ecol.* **27**, 955–964 (2016).
5. Lindström, L., Alatalo, R. V., Mappes, J., Riipi, M. & Vertainen, L. Can aposematic signals evolve by gradual change? *Nature* **397**, 249–251 (1999).
6. Gittleman, J. L. & Harvey, P. H. Why are distasteful prey not cryptic? *Nature* **286**, 149–150 (1980).
7. Exnerová, A. et al. Avoidance of aposematic prey in European tits (Paridae): learned or innate? *Behav. Ecol.* **18**, 148–156 (2007).
8. Mappes, J., Kokko, H., Ojala, K. & Lindström, L. Seasonal changes in predator community switch the direction of selection for prey defences. *Nat. Commun.* **5**, 5016 (2014).
9. Longson, C. G. & Joss, J. M. P. Optimal toxicity in animals: predicting the optimal level of chemical defences. *Funct. Ecol.* **20**, 731–735 (2006).
10. Stevens, M. & Ruxton, G. D. D. Linking the evolution and form of warning coloration in nature. *Proc. R. Soc. B Biol. Sci.* **279**, 417–426 (2012).
11. Marples, N. M., Kelly, D. J. & Thomas, R. J. Perspective: the evolution of warning coloration is not paradoxical. *Evolution* **59**, 933–940 (2005).
12. Riipi, M., Alatalo, R. V. & Lindström, L. Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. *Nature* **413**, 512–514 (2001).
13. Marples, N. M. & Mappes, J. Can the dietary conservatism of predators compensate for positive frequency dependent selection against rare, conspicuous prey? *Evol. Ecol.* **25**, 737–749 (2011).
14. McMahon, K. & Marples, N. Reduced dietary conservatism in a wild bird in the presence of intraspecific competition. *J. Avian Biol.* **48**, 448–454 (2017).
15. Lindström, L., Alatalo, R. V. & Mappes, J. Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behav. Ecol.* **10**, 317–322 (1999).
16. Endler, J. A. & Mappes, J. Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* **163**, 532–547 (2004).
17. Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193 (2005).
18. Lynn, S. K. Learning to avoid aposematic prey. *Anim. Behav.* **70**, 1221–1226 (2005).
19. Swynnerton, C. F. M. Birds in relation to their prey: experiments on wood hoopoes, small hornbills and a babbler. *J. S. Afr. Ornithol. Union* **11**, 32–108 (1915).
20. van de Waal, E., Borgeaud, C. & Whiten, A. Potent social learning and conformity shape a wild primate's foraging decisions. *Science* **340**, 483–485 (2013).
21. Landová, E., Hotová Svádová, K., Fuchs, R., Štys, P. & Exnerová, A. The effect of social learning on avoidance of aposematic prey in juvenile great tits (*Parus major*). *Anim. Cogn.* **20**, 855–866 (2017).
22. Snowdon, C. T. & Boe, C. Y. Social communication about unpalatable foods in tamarins (*Saguinus oedipus*). *J. Comp. Psychol.* **117**, 142–148 (2003).
23. Mason, J. R. & Reidinger, R. Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *Auk* **99**, 548–554 (1982).
24. Fryday, S. & Greig-Smith, P. The effects of social learning on the food choice of the house sparrow (*Passer domesticus*). *Behaviour* **128**, 281–300 (1994).
25. Johnston, A. N. B., Burne, T. H. J. & Rose, S. P. R. Observation learning in day-old chicks using a one-trial passive avoidance learning paradigm. *Anim. Behav.* **56**, 1347–1353 (1998).
26. Skelhorn, J. Colour biases are a question of conspecifics' taste. *Anim. Behav.* **81**, 825–829 (2011).
27. Harvey, P. H., Bull, J. J., Pemberton, M. & Paxton, R. J. The evolution of aposematic coloration in distasteful prey: a family model. *Am. Nat.* **119**, 710–719 (1982).
28. Alatalo, R. V. & Mappes, J. Tracking the evolution of warning signals. *Nature* **382**, 708–710 (1996).
29. Lindström, L., Lyytinen, A., Mappes, J. & Ojala, K. Relative importance of taste and visual appearance for predator education in Müllerian mimicry. *Anim. Behav.* **72**, 323–333 (2006).
30. Sillén-Tullberg, B. Higher survival of an aposematic than of a cryptic form of a distasteful bug. *Oecologia* **67**, 411–415 (1985).
31. Marchetti, C. & Drent, P. J. Individual differences in the use of social information in foraging by captive great tits. *Anim. Behav.* **60**, 131–140 (2000).
32. Aplin, L. M. et al. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541 (2015).
33. Hämäläinen, L., Rowland, H. M., Mappes, J. & Thorogood, R. Can video playback provide social information for foraging blue tits? *PeerJ* **5**, e3062 (2017).
34. Saitou, T. Ecological study of social organization in the great tit, *Parus major* L. III. Home range of the basic flocks and dominance relationship of the members in a basic flock. *J. Yamashina Inst. Ornithol.* **11**, 149–171 (1979).
35. Lee, T. J. & Speed, M. P. The effect of metapopulation dynamics on the survival and spread of a novel, conspicuous prey. *J. Theor. Biol.* **267**, 319–29 (2010).

36. Grüter, C. & Leadbeater, E. Insights from insects about adaptive social information use. *Trends Ecol. Evol.* **29**, 177–184 (2014).
37. White, S. L. & Gowan, C. Social learning enhances search image acquisition in foraging brook trout. *Environ. Biol. Fishes* **97**, 523–528 (2014).
38. Kis, A., Huber, L. & Wilkinson, A. Social learning by imitation in a reptile (*Pogona vitticeps*). *Anim. Cogn.* **18**, 325–331 (2015).
39. Galef, B. G. & Giraldeau, L.-A. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**, 3–15 (2001).
40. Heyes, C. M. Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231 (1994).
41. Skelhorn, J. & Rowe, C. Taste-rejection by predators and the evolution of unpalatability in prey. *Behav. Ecol. Sociobiol.* **60**, 550–555 (2006).
42. Olsson, A. & Phelps, E. A. Social learning of fear. *Nat. Neurosci.* **10**, 1095–1102 (2007).
43. Sasvári, L. & Hegyi, Z. How mixed-species foraging flocks develop in response to benefits from observational learning. *Anim. Behav.* **55**, 1461–1469 (1998).
44. Farine, D. R., Garroway, C. J. & Sheldon, B. C. Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Anim. Behav.* **84**, 1271–1277 (2012).
45. Nokelainen, O., Valkonen, J., Lindstedt, C. & Mappes, J. Changes in predator community structure shifts the efficacy of two warning signals in arctiid moths. *J. Anim. Ecol.* **83**, 598–605 (2014).
46. Farine, D. R., Montiglio, P. & Spiegel, O. From individuals to groups and back: the evolutionary implications of group phenotypic composition. *Trends Ecol. Evol.* **30**, 609–621 (2015).
47. Beckmann, C., Crossland, M. R. & Shine, R. Responses of Australian wading birds to a novel toxic prey type, the invasive cane toad *Rhinella marina*. *Biol. Invasions* **13**, 2925–2934 (2011).
48. Cremona, T., Spencer, P., Shine, R. & Webb, J. K. Avoiding the last supper: parentage analysis indicates multi-generational survival of re-introduced 'toad-smart' lineage. *Conserv. Genet.* **18**, 1475–1480 (2017).
49. Thorogood, R. & Davies, N. B. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science* **337**, 578–580 (2012).
50. Pruitt, J. N. et al. Behavioral hypervolumes of predator groups and predator–predator interactions shape prey survival rates and selection on prey behavior. *Am. Nat.* **189**, 254–266 (2017).
51. Orell, M. Population fluctuations and survival of great tits *Parus major* dependent on food supplied by man in winter. *Ibis* **131**, 112–127 (1989).
52. Snijders, L., Naguib, M. & van Oers, K. Dominance rank and boldness predict social attraction in great tits. *Behav. Ecol.* **28**, 398–406 (2017).
53. Guillette, L. M. & Healy, S. D. The roles of vocal and visual interactions in social learning zebra finches: a video playback experiment. *Behav. Process.* **139**, 43–49 (2017).
54. R Development Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, 2017).
55. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

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Author contributions

R.T. conceived the project and designed and conducted the experiments and analyses. J.M. designed the experiments and assisted with the analyses. H.K. conceived and conducted the modelling. All authors wrote the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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▸ Experimental design

1. Sample size

Describe how sample size was determined.	We set 30 birds as our minimum sample size based on degrees of freedom necessary for analysis. Final sample sizes were determined by availability of birds. Great tits become harder to catch during the late winter and become less motivated to finish experiments.

2. Data exclusions

Describe any data exclusions.	One bird was an outlier in 1 out of 3 analyses (Fig 1a); results are also presented with this data point included.

3. Replication

Describe whether the experimental findings were reliably reproduced.	15 birds were tested in each experimental group ("socially-informed" vs. "naive")

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.	Birds were caught randomly and assigned to experimental groups alternately by ID number (not the same as catching order).

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.	Blinding was not possible during the study as one author collected all experimental data.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	Data analysed using standard statistical methods, implemented in R.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	no unique materials were used

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	no antibodies were used

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	no eukaryotic cell lines were used
b. Describe the method of cell line authentication used.	no eukaryotic cell lines were used
c. Report whether the cell lines were tested for mycoplasma contamination.	no eukaryotic cell lines were used
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	no cell lines were used

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	Great tit, Parus major, collected from Konnevesi, Finland (62°37.7′N 026°17′E). Males & females used, both 1st year and older (10 females, 6 adults; 27 males, 15 adults, include 7 adult males as demonstrators).

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	study did not involve human participants